FLASH PATTERNS IN JAMAICAN FIREFLIES

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In most lampyrid fireflies the male flashes spontaneously in flight, whereas the female ordinarily remains at rest and flashes only in response to the flash of a male. It is well known that the flashing of male fireflies varies from species to species. The light differs in color, peak intensity and kinetics of emission (Harvey, 1952; Buck and Case, 1961; Seliger *et al.*, 1964) but the sequence and timing of flashing appear to be constant and species-specific. McDermott (1914) was the first to attempt to quantify these latter differences. The same notation was used by McDermott and Buck (1959) for their visual observations on 23 Jamaican species. In the latter paper the authors note that some species show variation in their flash patterns but add that the qualifications should not be allowed to obscure the really remarkable intraspecific constancy of the flash patterns, enabling the observer to recognize many of the species in free flight. Barber and McDermott (1951), in fact, used the visually observed flash patterns as an integral part of their attempt to sort out the North American species of *Photuris*. Visual observation cannot yield precise descriptions of flash contour and fine structure. These details are of particular importance, not only because they may serve as a more precise method of species identification, but because of their implications in regard to the ability of the photocyte and nervous system to control the underlying bioluminescent reaction. In the present work we therefore undertook to record the flashing by quantitative electronic means. Jamaica was chosen as the locale for operation because it provides a unique combination of the variety of firefly species characteristic of the moist tropics and terrain for field work which is both remote from artificial lights and safe for personnel. Furthermore, as already noted, there already exists a solid foundation of the taxonomic and histological work which is prerequisite for interpreting the physical data.

Material and Methods

Since fireflies usually flash spontaneously only during flight it was necessary to devise a photometer suitable for use in the field. In addition to the requirement of portability and humidity resistance of the electronic components the following requirements had to be met:

Signal-to-noise sensitivity

Coblentz (1912) reported the candlepower of the firefly flash to vary from 1/50 candela to 1/400 candela, with the predominating values being around 1/400

candela. While it is not proper to assess non-blackbody light intensities in photometric units of candelas we can make some estimates of the number of photons emitted per second by a "1/400 candela" firefly flash. One candela emits 4π lumens in all directions and the least mechanical equivalent of light is 0.00147 watts/lumen. This therefore corresponds to the emission of 4.6×10^{-5} watts, or at 5560 Å, the wave-length of maximum photopic luminus efficiency, to approximately 10^{14} photons per second. Firefly light therefore was the order of magnitude of the peak light intensity to be measured. At a distance of 15 feet the illumination would be 0.11×10^{-4} foot candles or 0.12×10^{-7} lumens/cm.^{2}. Moonlight, either direct or diffusely reflected, was to be avoided and ideally measurements were planned during the dark phase of the moon and in a direction pointing toward the dark sky or the vertical underbrush rather than directly down toward the grass. In addition there is the strong 5577 Å line of O_I present in the night sky.

With a phototube cathode area of 2 cm.^{2}, a peak illumination of 0.11×10^{-4} foot candles corresponds to a peak incident intensity of 10^8 photons per second. The dark noise of the phototube at maximum gain was equivalent to about 4×10^5 incident photons per second. This reasonably large signal-to-noise ratio permitted a 5440 Å interference filter, with a half width of 100 Å, to be used with the phototube. This permitted only a narrow green portion of the firefly emission spectrum to be detected, markedly reducing the signal-to-noise ratio. Furthermore this effectively reduced the contribution due to the 5577 Å O_I line. Under these conditions of filtering, an incident intensity of 2×10^8 photons/sec.-cm.^{2} of "pseudo-firefly" light, obtained by a method to be described in a later section, produced a signal equal to six times the phototube noise.

Acceptance angle

The firefly flash frequency is quite commonly as low as 10/minute and the flight velocity may easily be 2–5 feet per second. It is thus clear that the instrument should be able to monitor a radius of 20–30 feet if there is to be any reasonable chance of recording a sequence of three to four consecutive flashes from one individual. The usual firefly flight pattern is roughly straight and roughly parallel to the ground, but not sufficiently so that it is possible to predict exactly where, in the darkness, each successive flash of a given specimen will occur. Accordingly, the photometer needs to have a wide acceptance angle. This wide aperture, however, means background trouble from the general sky light. Fortunately this is less troublesome in the tropics than in regions with a long twilight.

In the resultant instrument a ½-inch diameter phototube (Dumont No. KM 2332) was used as the detector, gasket-sealed in a dural cylinder 8 cm. in diameter and 20 cm. long. By means of suitable diaphragms and collimators the phototube response was made flat over an acceptance solid angle of one steradian.

Time resolution

Even visually it is apparent that some species have a high-frequency flicker superimposed on the primary flash (*e.g.*, *Pyractomena lucifera* and *Photuris*

pennsylvanica in McDermott, 1914, and *Photinus ceratus, P. commissus* and *P. evanescens* in McDermott and Buck, 1959).

Further, half-rise time may be as little as 25 msec. (Brown and King, 1931; Snell, 1932; Alexander, 1943; Buck and Case, 1961). Accordingly, good time resolution is important in the photometer. The phototube electronic circuits are essentially the same as those used in previous measurements of marine bioluminescence (2, 3). A D.C. amplifier with a flat response up to 1000 c/s was used, together with a Sanborn two-channel Model 321 chart recorder, the latter having a flat response up to 100 c/s. The photometer unit, containing the phototube and the transistorized amplifier circuits, was connected to the control box through 15 feet of ¼-inch diameter flexible neoprene-covered cable.

Absolute photon calibration

The photometer was calibrated absolutely in photons/sec.-cm.^{2} in the following way: A National Bureau of Standards color temperature standard lamp was set up in combination with an empirically adjusted glass filter combination so that the resultant transmitted light had a spectral distribution very close to that of *Photinus pyralis*. This "pseudo-firefly" emission was obtained with the lamp operated at a color temperature of 2854° K and a composite filter combination consisting of Corning filters 1–69, 3–71, 3–76 and 4–96. Two centimeters of water in a Pyrex glass cell were used to absorb infrared energy. Using a thermopile, previously standardized with a National Bureau of Standards radiation standard lamp, the photometer was calibrated by means of a direct substitution technique.

The primary standardization of blackbody emission is based on energy emission. However, all reactions in photobiology are quantum phenomena and in any studies one is concerned with the number of photons involved. The steps in the conversion from the spectral distribution of firefly light and from the measurement of energy by the thermopile to photon flux are not immediately obvious. If the relative spectral distribution of *Photinus pyralis* bioluminescence is given by $f(\lambda)$, and the energy of a photon of wave-length in Angstroms is given by

$$E_\lambda = \frac{1987}{\lambda(\text{Å})} \times 10^{-18} \text{ Joule},$$

the average energy of the *P. pyralis* emission is given by

$$\langle E \rangle = 1987 \times 10^{-18} \frac{\int f(\lambda)/\lambda \, d\lambda}{\int f(\lambda) d\lambda} \text{ Joule},$$

where the integration is performed over the entire emission spectrum. Therefore, if W is the energy flux in watts/cm.^{2} measured by the thermopile at a fixed distance from the "pseudo-firefly" source, the photon flux is given by

$$I = \frac{W}{\langle E \rangle} \text{ photons/sec.-cm.}^2$$

At this same fixed distance but with an attenuation filter the photometer response was measured so that any scale reading could be converted to incident photons/sec.-cm.^{2} effectively emitted by *P. pyralis*. The fact that other fireflies have slightly different spectral distributions affects the accuracy of the measurements since each spectral distribution has a slightly different value of $<E>$. However, the errors introduced by assuming that all fireflies examined have a *P. pyralis* emission spectrum is of the order of 10–20% and is well within the uncertainties due to measurements of distances in the field during a flashing event. Even these errors can be corrected for if necessary since, as can be seen, I is inversely proportional to $<E>$.

From the absolute calibration and the complete flashing record it is also possible to obtain the total number of photons emitted per firefly flash.

Because of the precipitous jungle-covered terrain, roads provided almost the only localities flat and open enough for repetitive measurements. The species studied were beetles of the lampyrid genera *Lecontea, Photinus, Photuris* and *Diphotus,* and the elaterid bettle *Pyrophorus.* Except for *Lecontea gamma* and *Photinus commissus,* which were studied on Castle Hill, about a mile northwest of Long Bay, the records were made at an altitude of about 750 feet, on a remote section of the Ecclesdown Road, that runs through the foothills of the John Crow Mountains (Portland Parish). Fireflies were chosen that were flying along a straight stretch of the road. In making records one investigator attempted to keep the phototube directed at and close enough to the chosen firefly, a second monitored high voltage to the phototube of the photometer and operated the recording meter, and the other participants hovered nearby with insect nets, ready to capture the specimen as soon as the recordings were completed or the insect showed signs of flying off the road. As soon as a specimen was captured it was put in a vial for later identification from the key of McDermott and Buck, and given a number corresponding to that of the record chart.

Results

Representative records of flashing behavior are presented in Figures 1 through 5. In viewing these it must be kept in mind that although the time scale (abscissa) is accurate, light intensity varies with distance from specimen. Attention is directed particularly to the following points:

A. *General flash patterns.* At the outset it is to be recalled that fireflies that have a light organ structure involving a regularly arranged tracheal supply, and tracheal end-cells (*Photinus, Photuris*) typically produce short sharp flashes, whereas those lacking end-cells (*Diphotus, Pyrophorus*) emit their light as long lingering glows (Buck, 1948). Among flashing-type lampyrids, we find luminosity in flight to vary from the single and usually homogeneous flashes of *Photinus melanurus* (Spec. 91, 20 Figure 3) and *P. leucopyge* (Spec. 5, 12 Figure 2), sometimes delivered with remarkable regularity, through the compound or flickering flashes of *Lecontea gamma* (Spec. 72 Figure 1), *Photinus evanescans* (Spec. 110B Figure 1, 125 Figure 1, 130 Figure 1), *P. gracilobus* (Spec. 132, 108 Figure 1), *P. lobatus* (Spec. 42 Figure 3) and *Photuris jamaicensis* (Spec. B Figure 4),

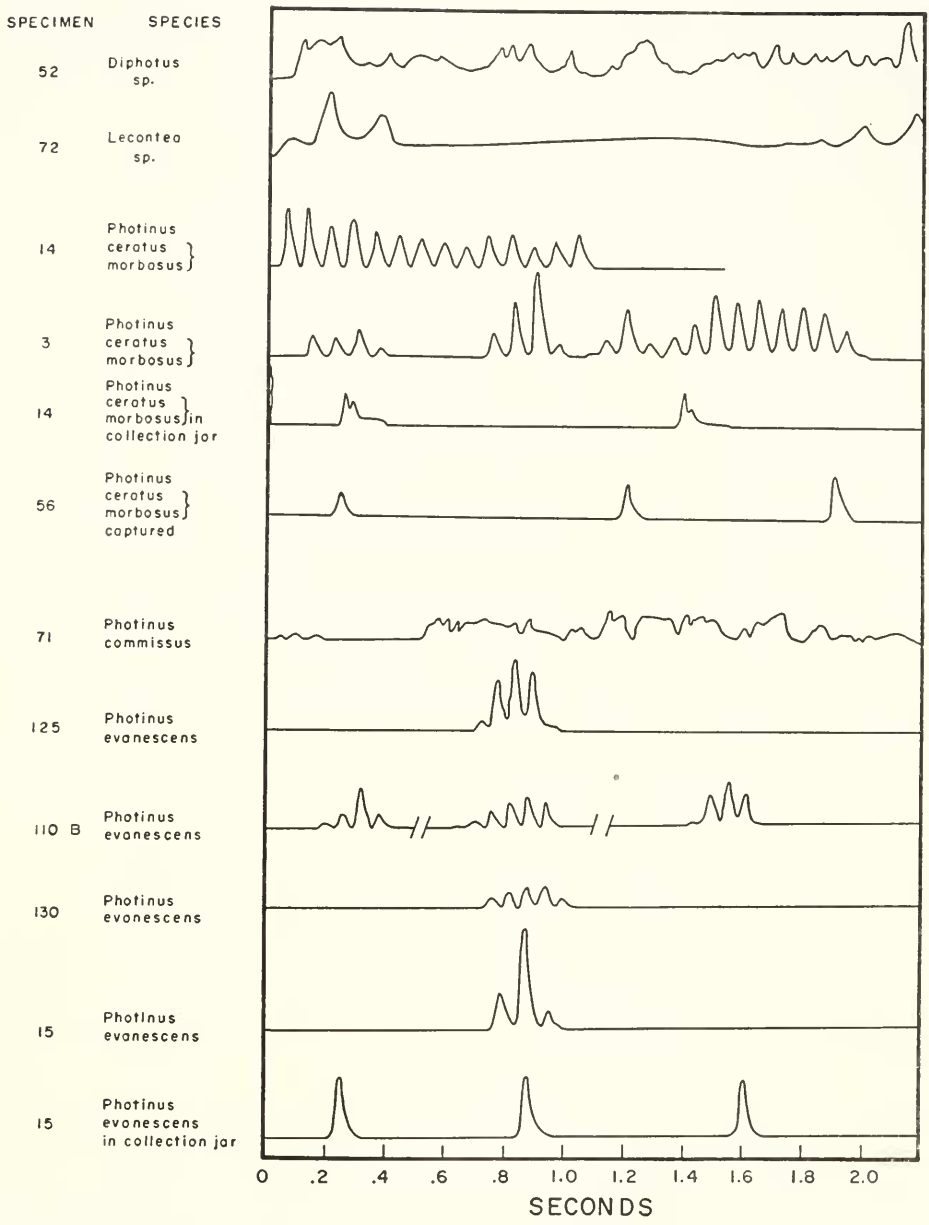

FIGURE 1. Direct tracings of field recordings of firefly flash patterns for *Diphatus* sp., *Lecontea* sp., *Photinus ceratus-morbosus, Photinus commissus* and *Photinus evanescens.*

to the complex pattern of *Photinus ceratus-morbosus*, in which two short flickers and a long flicker are grouped together (Spec. 3 Figure 1).

In contrast, the glowing types of firefly, *Diphotus sp.* (Spec. 52 Figure 2) and *Pyrophorus plagiophthalamus* (Spec. C, D, E, F, G Figure 5), showed light-production of the greatest irregularity. This unexpected finding (the light of both insects appears quite steady to the eye) will be discussed below. The causation of the similar record made by a flying female of *Photinus commissus* (Spec. 71 Figure 1) will be considered at the same time, but the phenomenon is not entirely surprising in view of the visual observation that female lampyrids, on the rare occasions when they do take wing, not infrequently show an irregular

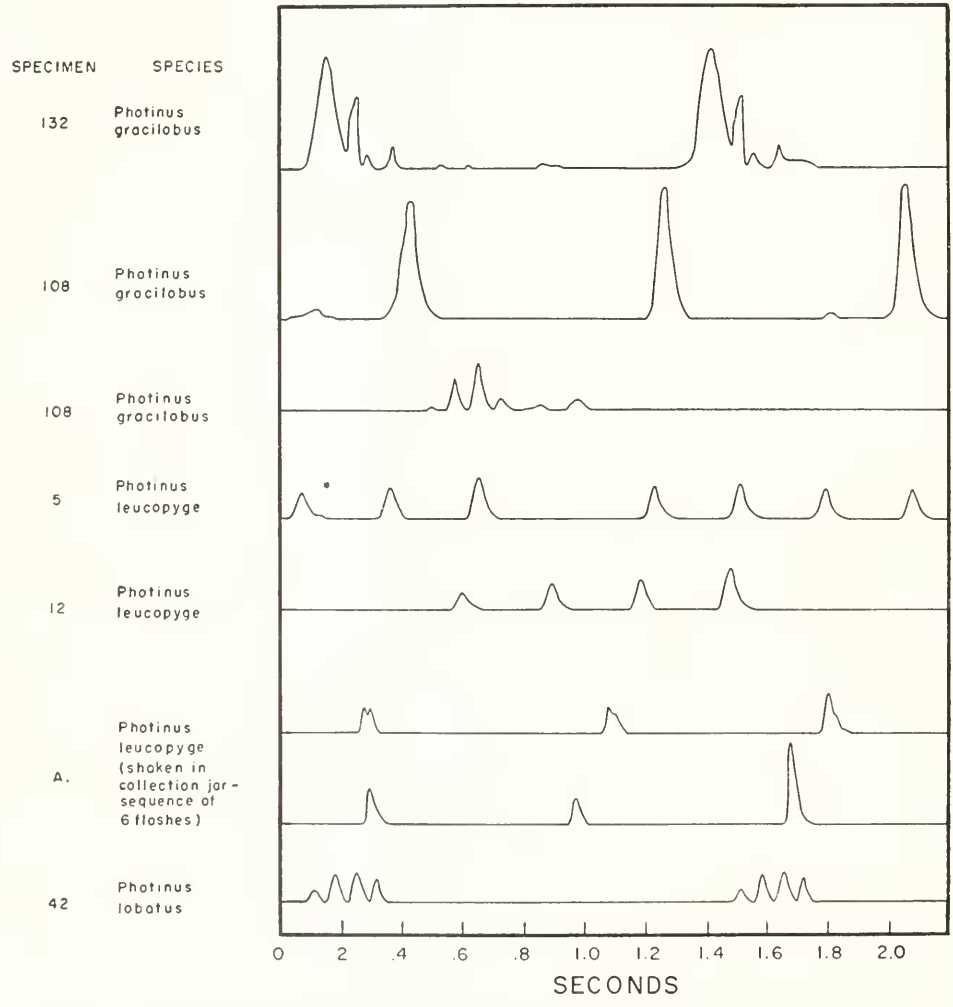

FIGURE 2. Direct tracings of field recordings of firefly flash patterns for *Photinus gracilobus*, *Photinus leucopyge* and *Photinus lobatus*.

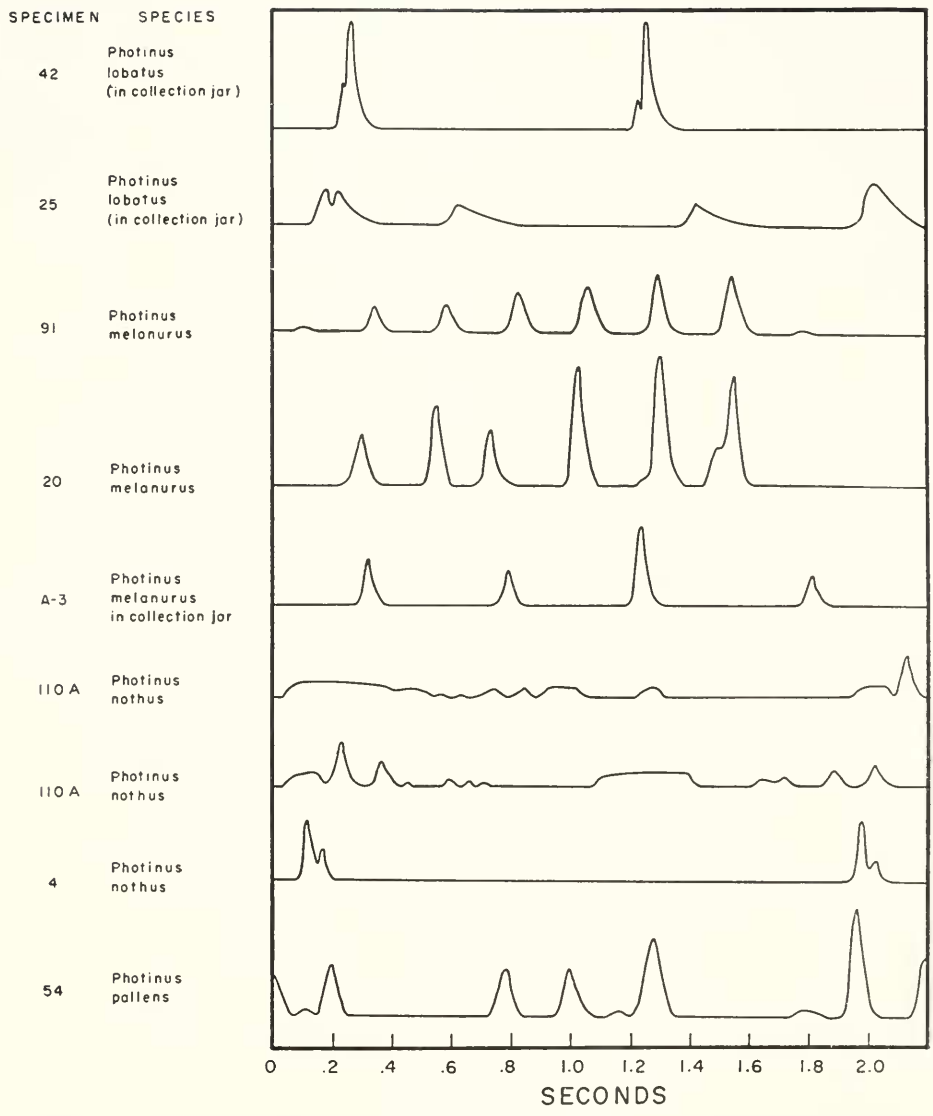

FIGURE 3. Direct tracings of field recordings of firefly flash patterns for *Photinus lobatus, Photinus melanurus, Photinus nothus* and *Photinus pallens.*

glow (*e.g.,* see remarks of Buck and Case, 1961, in reference to a North American photurid). It is likewise not wholly unexpected to find similar irregular glowing between the flashes of occasional flying males, for example *Photinus gracilobus,* (Spec. 132 Figure 2) and *P. pardalis,* (Spec. 129 Figure 4), since such "intercalated flashlets" were seen in several species by McDermott and Buck. However, records for Spec. 71 (Fig. 1) (*Photinus evanescens*) and Spec. 110A

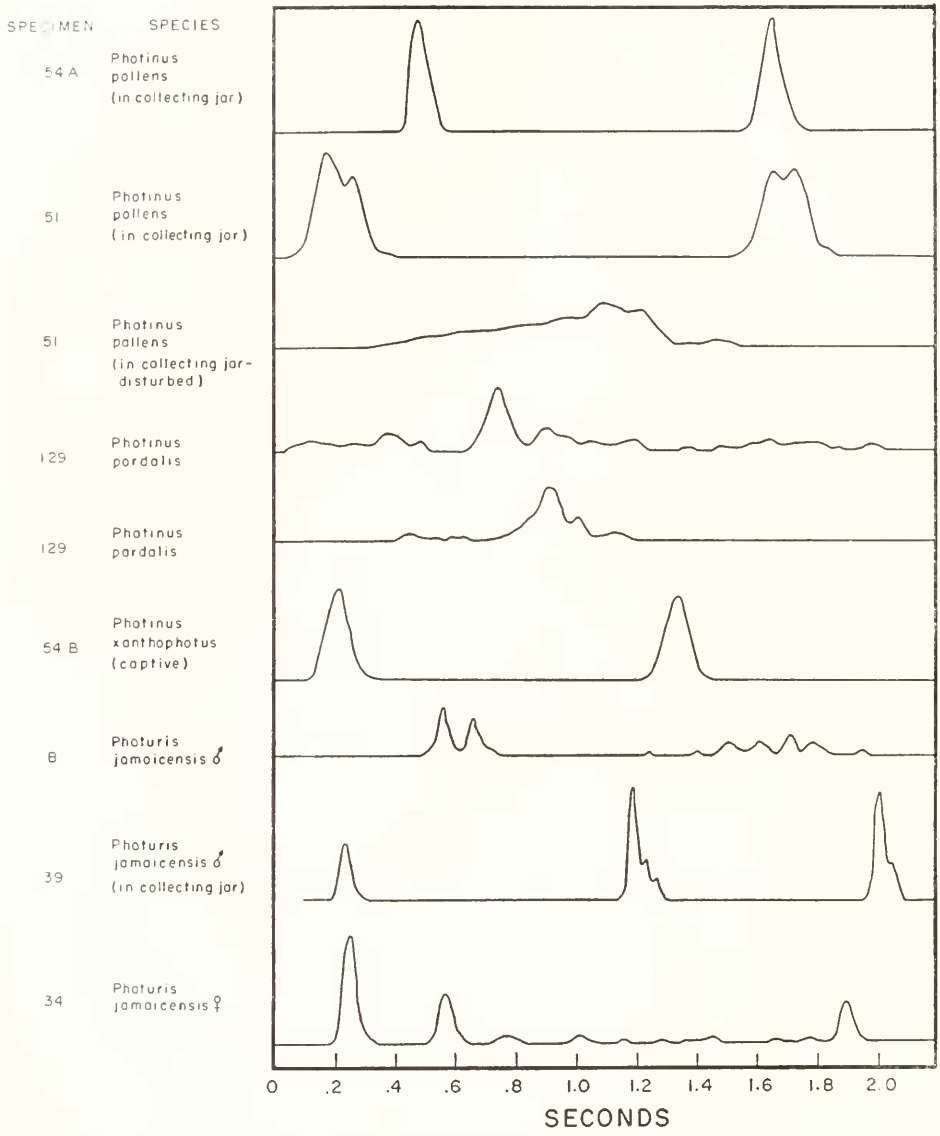

FIGURE 4. Direct tracings of field recordings of firefly flash patterns for *Photinus pallens*, *Photinus pardalis*, *Photinus xanthophotus* and *Photuris jamaicensis*.

(Fig. 3) (*P. nothus*) must be regarded as definitely atypical in their irregularity and paucity of clearly defined major flashes.

B. *Flashing in captivity.* As noted also by McDermott and Buck, there is often a pronounced difference between the flashing of male lampyrids in flight and in captivity. In general the change is in the direction of producing single flashes where the flight pattern is compound—for example Spec. 56 (Fig. 1) *vs.* Spec.

14 (Fig. 1) (*P. ceratus morbosus*), Spec. 15 (Fig. 1) *vs.* Spec. 110B (Fig. 1) (*P. evanescens*) and Spec. 25 (Fig. 3) *vs.* Spec. 42 (Fig. 3) (*P. lobatus*)—which corresponds to the field observation that fireflies at rest on bushes tend to flash singly, and at irregular intervals. However, we also recorded instances in which the captive animal produced a more complex flash than typical for flight—*e.g.,* Spec. 51 (Fig. 4) *vs.* Spec. 54A (Fig. 4) (*P. pallens*), Spec. 39 (Fig. 4) *vs.* Spec. B (Fig. 4) (*Photuris,* male) and Spec. 50 (Fig. 5) *vs.* Spec. 34 (Fig. 4) (*Photuris,* female). Unfortunately we did not record the amount of mechanical stimulation (shaking or jarring), if any, needed to induce flashing, so nothing

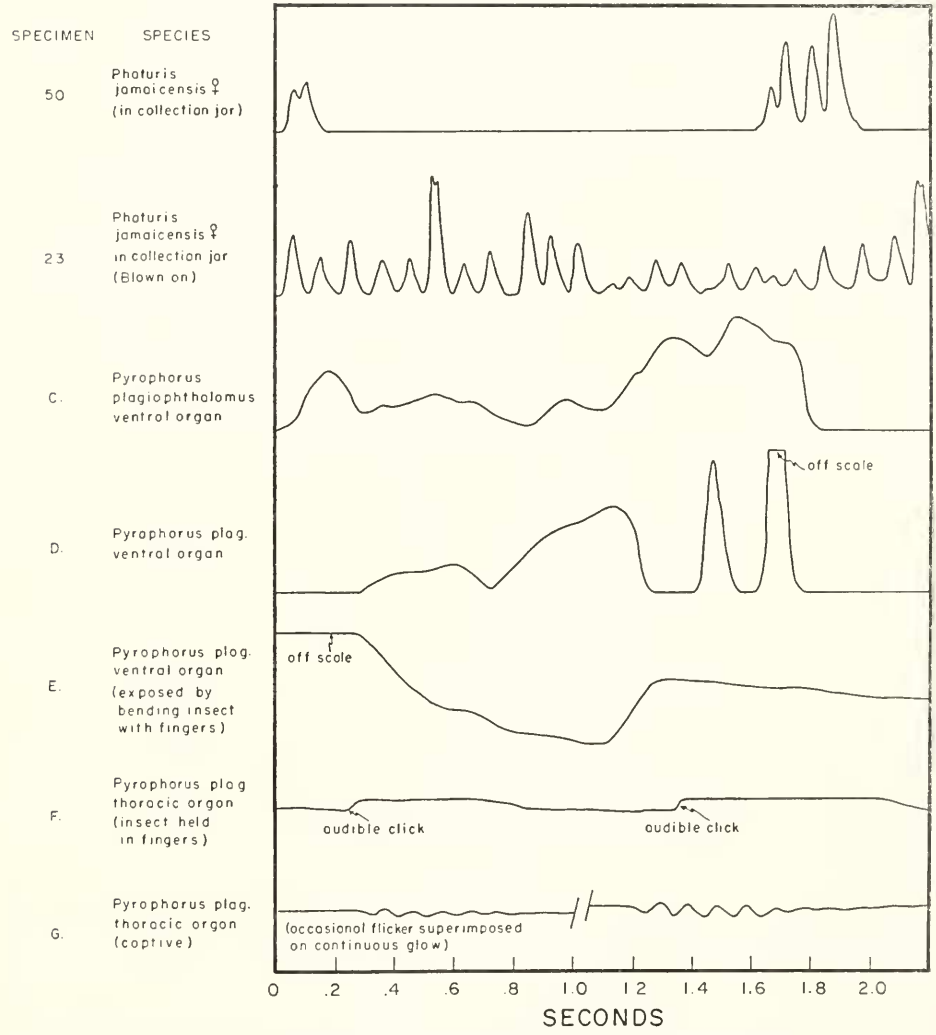

FIGURE 5. Direct tracings of field recordings of firefly flash patterns for *Photuris jamaicensis* and *Pyrophorus plagiophthalamus.*

can be said about the conditions for neural stimulation of flashing during flight *vis à vis* quiescence. It is, however, clear that the insects have the power of varying their flash pattern to a considerable extent.

C. *Variability and its taxonomic implications.* McDermott and Buck reported significant differences in flash patterns within certain species in regard to populations from different localities—*e.g.*, lowland *versus* mountain—and even occasionally between individuals from the same population. The present photometer records confirm this impression. It appears, therefore, that while the flash pattern has no absolute significance as a criterion of identification it can be a valuable supplement to the standard taxonomic characters which are themselves no less variable (Buck, 1942). A case in point is the species complex, *Photinus ceratus-morbosus*, erected as separate species by Barber (1941), redescribed by McDermott and Buck but without achieving a really sharp separation, and not separable in our present sample on the basis of either morphology or flashing behavior. Nonetheless our general experience has been to confirm solidly a specific individuality of many of the flash patterns and a pragmatic value in identification of the same order of consistency and usefulness as bird calls have for the ornithologist.

D. *Relation to visual records.* There is good agreement between our present photometer records and the visual observations of McDermott and Buck. In instances such as *P. evanescens*, *P. nothus*, *P. ceratus-morbosus* and *Photuris*, the eye recognizes the "flickering" or "twinkling" nature of minute light sources of low absolute intensity fluctuating of the order of 15 times per second. It is interesting, however, that the eye judges the variation in intensity between peak and trough to be very minor—a mere ripple in a plateau level of luminescence (McDermott and Buck, Fig. 1)—whereas the photometer shows the individual peaks of the compound flashes to be very well separated, intensity falling nearly or quite to extinction in the troughs.

In certain instances our records show the eye to have been at fault. The inadequacies were of two main kinds. First, some real twinkles were not resolved. For example, the short four-peak forerunners of the main 12–14-peak twinkle of *P. ceratus-morbosus* were seen as single flashes, dimmer than the main twinkle (see also McDermott and Buck, *ceratus* type 3c). This is strange in view of the success in resolving visually the apparently similar twinkles of *P. evanescens* (Spec. 110B, 125 Fig. 1), particularly since McDermott and Buck reported a twinkle sometimes so rapid as to look like a single flash or glow from a distance. Similarly the compound flash of *P. gracilobus* (Spec. 132 Figure 2) looks single. In the latter instance the failure to discriminate the separate peaks could well be due to the dominant intensity of the first and the incomplete extinction between the sub-peaks.

The display of *P. lobatus* (Spec. 42 Figure 3) is at variance with the single flash given by McDermott and Buck as typical of the lowland variety of this species. It does agree with the twinkle reported for the high-mountain form in summer observations, suggesting the interesting possibility of a migration to lower altitudes during the "winter" season; but unfortunately in the hurly-burly of recording from and capturing Spec. 42 we failed to note what was the visual impression of his flash. In this connection, incidentally, the triple twinkle of *P.*

ceratus-morbosus is also the high-altitude variant of this species (*ceratus*) according to McDermott and Buck.

In the second and more interesting discrepancy between visual and photometer records, the eye sometimes saw twinkles where the photometer saw none (*e.g., P. leucopyge*). This is not as isolated a discrepancy as may appear because McDermott and Buck specifically note ". . . possibly a high-frequency flicker . . ." for three species which they reported as having a single flash (*Photinus lewisi, P. naevus* and *P. synchronaus*). To add to the physiological interest of the question it is the strong impression of one of us (J. B.) that illusion of flicker is much stronger when a "flash" is seen in peripheral vision. The question is presently under separate investigation.

E. *Parameters of flash control.* The records of flashing indicate some of the potentialities of the mechanism controlling luminescence. For example, we see that the neural pacemaker that times the individual flashes during flickering can fire with remarkable regularity and at frequencies ranging from 10 to 18 per second in different species (Spec. 4 Figure 3, 23 Figure 5; 14, 3 Figure 1; 42 Figure 3; 125, 110B, 130 Figure 1). Similarly the kinetics of the individual flashes show that the neuroeffector control of the individual photocytes must be of a high order since the many thousand cells comprising the lantern can all complete their cycles of activity within 50–100 msec. Though, as mentioned earlier, the relative intensity of major flash episodes may be influenced by changing distance of the insect from the photometer, this factor should have little effect on records on the high frequency flashing within episodes of twinkling. Hence, the apparently consistent differences in relative intensity of the individual peaks within the flicker of *P. evanescens* (Spec. 125, 110B, 130 Figure 1) and *P. gracilobus* (Spec. 132 Figure 2), for example, probably represent a valid second order of species-specific neuroeffector programming of luminous emission. On the other hand, the intensity fluctuations within the long twinkles of *P. ceratus-morbosus* (Spec. 14, 3 Figure 1) and the *Photuris* female (Spec. 23 Figure 5) show that the emission is capable of spontaneous variation.

F. *Implications of variation in glow level.* Intensity fluctuations during long-continued luminescence are of special interest. Forms such as *Diphotus*, which lack the ability to produce a sharp brief flash, are nevertheless unexpectedly found to have variations in intensity superimposed on their continuous luminescence (Spec. 52 Figure 1). The fact that these variations are not detected by the eye is probably due to their small magnitude relative to the continuous luminescence and to the small change between successive peaks. However, the frequency of fluctuation equals or exceeds that seen in species able to produce concerted flashes. A clue to a possible mechanism is provided by analogy with the dim luminescence that is occasionally seen between the successive flashes of the usual lampyrid pattern. Microscopic examination of the lantern surface shows that this light is sometimes due to a generalized dull steady glowing of the luminous tissue, but sometimes also to numerous sparkling points, flashing on and off briefly and irregularly. This punctate "scintillation," studied at about 100 diameters magnification by Case and Buck (1963) in lanterns irrigated with eserin solution, was attributed to both single photocytes and small aggregations. This suggests, therefore, that both the irregular luminescence recorded from some individuals of

flashing-type fireflies (*e.g., P. commissus,* Spec. 71 Figure 1; *P. gracilobus,* Spec. 132 Figure 2; *P. nothus,* Spec. 110A Figure 3 and *P. pardalis,* Spec. 129 Figure 4), and that recorded from the glowing *Diphotus,* could be due to asynchronous and sporadic firing of small aggregations or photocytes.

The luminescence of *Pyrophorus* presents an especially interesting problem. Both the dorsal thoracic and ventral abdominal organs in this remarkable beetle, in captive specimens, seem to glow absolutely steadily, and nothing resembling flashing was ever seen in the field. The recordings made from individuals in flight (*i.e.,* from the abdominal organ) typically show great, though slow, fluctuations in intensity (Spec. C, D, E Figure 5). These are readily explained in terms of the great speed and erratic course of the insect's flight. (The two apparent flashes near the end of Spec. D may possibly be an unexplained exception but even these seem readily interpreted as "tracking errors" of the operator in his frantic efforts to keep the photometer pointed at the specimen.) In any case there is no indication of fine structure in rate of change of intensity, nor is there, some-

TABLE I

Light intensity emitted by various fireflies

Species	Peak Photon Intensity	Total Photons per Flash
Photinus ceratus-morbosus	14×10^{12}/sec	0.4×10^{12}
Photinus lobatus	17.5	1
Photinus pallens	18	2.4
Photinus xanthophotus	108	10
Photinus jamaicensis	52.5	3.4
Photinis jamaicensis	28	0.7
Photinus jamaicensis (blown on—excited)	112	2.8
Pyrophorus plagiophthalamus (thoracic organ)	100	Emits continuously

times, in the glowing of the thoracic organ in captive animals (Spec. F Figure 5). However, in some instances the photometer does detect a rapid, regular, small-amplitude pulsation superimposed on the continuous glow (Spec. G Figure 5). Harvey (1931), by the use of a string galvanometer, recorded what is apparently the same phenomenon though with a somewhat lower frequency (6 per second at first, decreasing in 15 seconds to 2.5 per second). In any case, this apparently well coordinated control, approaching in frequency the best achieved by fireflies with tracheal end-cells, poses an important question for future investigation.

G. *Absolute photon emission.* The absolute photon efficiency of the photometer was determined for the North American firefly, *Photinus pyralis,* by the method described previously. Using this calibration it was possible to determine both the maximum light intensity and the total light quanta emitted per flash for a number of Jamaican species. The specimen was held or agitated in a glass jar at a measured distance from the phototube in a dark room. The results are presented in Table I. It is surprising that there is only about an 8-fold variation in peak intensity, not obviously correlated with size of lantern, and that there is

no distinction in this respect between glowing-type fireflies (*Pyrophorus*) and flashers. The total photon emission should reflect the mass of photogenic tissue and flash duration, and would be expected to vary widely.

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Summary

1. A portable photometer has been devised, permitting recording of flashes of flying fireflies in the field under natural conditions.

2. Various Jamaican fireflies typically emit their light according to one of the following patterns: (a) long-continued flow, usually fluctuating in intensity, (b) single concerted flashes of 75–100-msec. duration, delivered at regular intervals of 2 to 6 or more seconds, (c) one or more twinkles or flickers consisting of 4–20 or more short flashes at frequencies of 10–18 per second, delivered every few seconds.

3. In captivity a given species usually gives a simpler type of flash than when in flight.

4. The flash patterns are highly constant and are characteristic of particular species, though not completely invariant.

5. The photometric records show some visual impressions of firefly flash type to be in error, particularly in the detection of flicker.

6. The photometric records show that the photogenic control mechanism is capable of inducing peak flash luminosity or of extinguishing the light in periods of the order of 30–60 msec.

7. Unexplained high-frequency fluctuations in intensity of glowing are provisionally attributed to uncoordinated firing of photocytes in small groups.

8. Data for absolute photon emission are given for six species.

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